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Soil autotrophic and heterotrophic respiration respond differently to land-use change and variations in environmental factors

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ABSTRACT

Converting natural forests to intensively managed plantations markedly alters soil carbon (C) dynamics. However, the impact of such land-use change on soil respiration (R_S) components remains unclear. The objective of this study was to examine the effect on R_S, autotrophic respiration (R_A) and heterotrophic respiration (R_H) of converting a natural evergreen broadleaf forest to an intensively managed Moso bamboo (*Phyllostachys edulis*) plantation. A two-year field study was carried out to assess the seasonal dynamics of R_S, R_A and R_H in three broadleaf forest-bamboo plantation pairs, using a portable soil CO_2 flux measurement system. Results showed that converting the evergreen broadleaf forest to the bamboo plantation increased the annual cumulative R_S and R_H by 18.8% and 20.9%, respectively, but did not change the annual cumulative R_A. Soil temperature alone explained 48% and 79% of seasonal variations in R_A and R_H, respectively, in the evergreen broadleaf forest, and 68% and 79%, respectively, in the bamboo plantation. The land-use change increased the apparent temperature sensitivity (Q_{10}) of R_A, but did not affect that of R_H. Regardless of the land-use type, both R_A and R_H were positively correlated with soil water soluble organic C, but not with soil moisture content. The R_H was positively correlated to soil microbial biomass C (MBC) in the evergreen broadleaf forest, but not in the bamboo plantation. The R_A was not correlated with soil MBC, regardless of the land-use type. Therefore, soil R_A and R_H responded differently to land-use change and variations in environmental factors, suggesting that partitioning of R_S to different components is essential to elucidate mechanisms associated with changes in R_S induced by land-use change and to predict R_S under different climate change scenarios.

1. Introduction

Forests play a key role in carbon (C) cycling in terrestrial ecosystems and mitigation of global climate change (Fang et al., 2001; Zhou et al., 2006; Wood et al., 2012). The soil organic C (SOC) stock in the world is much greater than the atmospheric C stock or vegetation C stock (Batjes, 1996), and the C stored in forest soils is estimated to be 70% of the global SOC (Jandl et al., 2007), implying that a small change in the C stock in forest soils would substantially alter the atmospheric CO_2 concentration (Peng et al., 2008). Soil respiration (R_S) is one of the most important processes of carbon (C) efflux from the soil system to the atmosphere (Xu and Shang, 2016). The annual global CO_2 emission from R_S is much higher than that from fossil fuel combustion (Bond-Lamberty and Thomson, 2010). Therefore, the change in R_S will greatly alter the ecosystem C cycle, which could consequently affect the global climate change (Xu and Shang, 2016).

The R_S consists of autotrophic (R_A) and heterotrophic respirations (R_H) (Baggs, 2006). The R_A originates from roots and the rhizosphere, and is mainly influenced by fine root biomass, soil temperature, nutrient availability, C allocation and stand age (Arevalo et al., 2010; Hopkins et al., 2013; Cheng et al., 2015; Wang et al., 2017). In contrast, R_H originates from soil microbes and soil fauna decomposing soil organic matter (SOM) and plant litter, and is mainly affected by soil temperature, moisture content, organic C pool size and microbial biomass (Hanson et al., 2000; Arevalo et al., 2010; Yan et al., 2015a; Huang et al., 2016; Li et al., 2017). The R_A to R_S ratio generally ranges from 10% to 90% (Bond-Lamberty et al., 2004; Subke et al., 2006), and is affected by biotic and abiotic factors such as plant vegetation type, soil type, management practices, stand age, and climate conditions (Bond-Lamberty et al., 2004; Saurette et al., 2008; Tu et al., 2013; Yan et al., 2015a; Balogh et al., 2015; Huang et al., 2016; Wang et al., 2017). Therefore, quantifying R_S components can help elucidate

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mechanisms involved in the change of R_S in response to altered biotic and abiotic factors.

Land-use change is one of the most important factors affecting R_S (Don et al., 2011), and there are large variations in the response of R_S to land-use change. Sheng et al. (2010) demonstrated that the mean annual R_S was decreased by 32.3% following the conversion of natural forests to secondary forests, and by 48.3% and 45.7% after the conversion of natural forests to Chinese-fir and *Schima superba* plantations, respectively. Guo et al. (2016) reported that converting natural forests to Chinese-fir and *Pinus massoniana* plantations decreased the annual R_S, while increased the apparent temperature sensitivity of soil respiration (Q_{10}). In contrast, Liu et al. (2011) showed that converting natural evergreen broadleaf forests to intensively managed Moso bamboo (*Phyllostachys edulis*) plantations significantly increased the annual R_S. Shi et al. (2015) reported that converting primary forests to larch and pine plantations increased the average R_H by 31% and 19%, respectively, while such land-use change did not affect the $R_{A.}$ The discrepancy regarding land-use change effects on R_S and its components would be attributed to the difference in plant species composition or vegetation type, management practices applied and climate conditions among different studies (Sheng et al., 2010; Liu et al., 2011; Shi et al., 2015).

Natural evergreen broadleaf forests are an important natural forest resource in the subtropics. However, under long-term anthropogenic disturbance, such forests have been decreasing in the last two decades (Yang et al., 2014). In southern China, a portion of evergreen broadleaf forests have been transformed to intensively managed forests with valuable forest products due to their high economic return to farmers (Li et al., 2014; Guo et al., 2016). Moso bamboo (*Phyllostachys edulis*) is extensively distributed across many provinces in southern China, and most of the bamboo forests are intensively managed (Li et al., 2013b; Yan et al., 2015b). Owing to the substantial economic benefit from the cultivation of Moso bamboo plantations, a considerable portion of natural evergreen broadleaf forests in some regions have been converted to such plantations (Li et al., 2013b; Fang et al., 2017). Intensive management in the Moso bamboo plantation includes inorganic fertilizer application, deep tillage, and understory vegetation removal (Song et al., 2011). The aforementioned conversion is expected to markedly alter soil physical, chemical and biological properties due to the changed vegetation characteristics and management practices. However, the effect of such land-use conversion on the R_S components has been poorly understood.

The purpose of this study is to examine the impact of converting a natural evergreen broadleaf forest to an intensively managed Moso bamboo plantation on R_S and its components. Specifically, the following hypotheses were tested: (1) converting natural forests to bamboo plantations increased soil R_A and R_H, due to the accelerated decomposition of SOM and enhanced plant growth caused by the intensive management practice applied in the Moso bamboo plantation; (2) soil R_A and R_H differently respond to the variation in environmental factors; and (3) the land-use change modifies the relationships between R_S components and environmental factors. This research will help understand the implications of converting natural forests to intensively managed plantations on ecosystem C balance.

2. Materials and methods

2.1. Experimental sites

The study was carried out at an experimental site in Shankou Township (30°14′N, 119°42′E), Lin'an City, Southeast China. The site is located in a hilly area with an elevation of ~150 m. The climate of this region is subtropical with an annual mean temperature of 15.8 °C between 2004 and 2013, 1946 h of annual sunshine, and 239 days of frost-free period. The monthly mean air temperature and monthly cumulative precipitation from April 2013 to March 2015 are shown in Fig. 1. Soils at the experimental site are classified as Ferralsols according to the FAO soil classification system (WRB, 2006).

Two land-use systems, i.e., natural evergreen broadleaf forests and Moso bamboo plantations, were selected for this study. In the broadleaf forest, the main tree species were *Cyclobalanopsis glauca*, *Castanopsis eyrei* and *Castanopsis sclerophylla*, with an overall canopy cover of 70%. Understory vegetation mainly included *Litsea cubeba*, *Lindera glauca*, and *Camellia cuspidate*, with an 85% ground coverage. The density of broadleaf forest was 3860 stem ha^{-1}, based on the number of trees that had a diameter at breast height (DBH) more than 1 cm. The intensively managed bamboo plantations were converted from natural evergreen broadleaf forests in 2002. Stocking density in these plantations was 2950 culm ha^{-1}, and the mean diameter at breast height of the bamboo plants was 10.1 cm. In June of every year, fertilizers, including urea (200 kg N ha^{-1}), super phosphate (60 kg P ha^{-1}) and potassium chloride (70 kg K ha^{-1}) were broadcast applied, followed by tillage to 30–35 cm depth. The ground vegetation in the bamboo plantation was manually removed each year.

2.2. Experimental design

The paired-plot approach was used to study the effect of land-use change. Each paired plot had the same geographic and environmental factors, including soil type, slope (15–20°) and aspect (south), and so on. At three different locations of this experimental site, two adjacent plots (one in a natural evergreen broadleaf forest and the other in a Moso bamboo plantation) were established in 2012. All of the above-mentioned plots were located within a ~3 km^2 area. The distance between the broadleaf forest and the adjacent bamboo plantation in each pair was < 100 m. The soil texture in the two land-use systems in each pair was similar (Table 1), suggesting that the two paired plots had the soil type/properties before the land-use change. Each plot was 400 m^2 (20 × 20 m). Soil samples were taken from the 0–20 cm depth from five randomly selected points in each plot with a corer. The five soil samples collected from each plot were mixed to form a composite sample for each plot. Before the soil sampling, the litter layer on the mineral soil surface was removed. The soil samples were placed on ice in a cooler and transported to the laboratory, where they were passed through a 2 mm sieve. Visible roots and stones were removed from the samples. One half of the sieved fresh sample was stored in a refrigerator at 4 °C, and another half was air-dried. Soil bulk density samples were also collected using a bulk density corer with a 200 cm^3 volume to determine the soil bulk density of each plot.

The trenching technique was used to partition total R_S into R_A and R_H. Three polyvinyl chloride (PVC) collars with a coverage area of 314 cm^2 (diameter 20 cm) and a height of 11.5 cm were randomly inserted into the soil in each non-trenched subplot; this was used to determine the total R_S. Three trenched subplots (1 × 1 m) were established near the non-trenched subplots by digging a trench 15 cm wide and 70 cm deep, below the main tree rooting zone. Four 1 × 1 m PVC panels were inserted into the trench to stop roots from growing into the trenched subplots, and the trench was backfilled. Another three PVC collars with the same size as the previous ones were installed in the center of the trenched subplots to determine R_H. All collars were inserted 2–2.5 cm into the soil, about 0.5 m from the basal part of tree or bamboo plants.

To minimize the trenching effect on soil disturbance and effect of dead root decomposition in the trenched subplots on R_S, we began to measure R_S in April 2013, 8 months after trenching. In the trenched subplots, vegetation in the inner area of collars was periodically removed manually throughout the experiment to ensure no root growth.

2.3. Measurement of R_S

During the two years (April 2013 to March 2015), R_S was measured twice a month between 9:00 a.m. and 11:00 a.m. on clear mornings. The CO_2 efflux and soil temperature (at 10 cm depth) data were

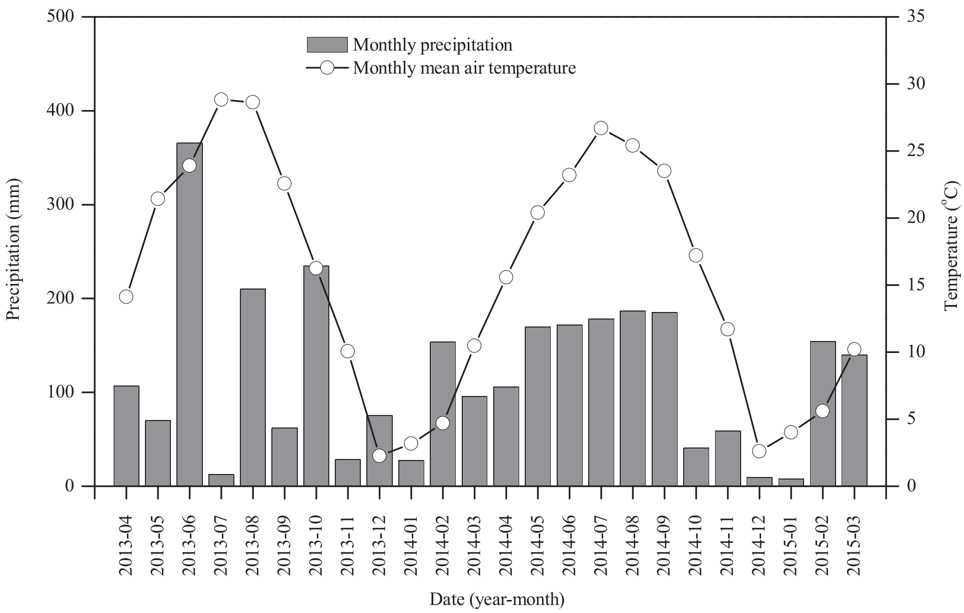

Fig. 1. Monthly precipitation and monthly mean air temperature during the study period.

measured by a LI-8100 soil CO_2 flux system (LI-COR Inc., Lincoln, Nebraska), equipped with a temperature probe. For each collar, soil CO_2 efflux was measured twice. The time for each measurement was 90 s, separated by 30 s between repeated measurements, during which the chamber opened and closed automatically to achieve ambient CO_2 concentrations.

2.4. Measurement of soil physicochemical properties

Selected physical and chemical properties of soil samples taken from each plot at the beginning of this study were determined as follow. Soil pH was measured in a 1:2.5 (w:v) mixture of soil and distilled water. Soil organic C (SOC) and total N (TN) concentrations were measured with an elemental analyzer (CHN-O-RAPID, Heraeus, Germany). Available P (extracted by a mixed solution of 0.03 mol L^{-1} NH_4F and 0.025 mol L^{-1} HCl) concentration was determined by the Bray procedure (Bray and Kurtz, 1945). Available K (extracted by 1 mol L^{-1} NH_4OAc) concentration was determined by the flame photometric method (Zhang et al., 2014). The soil sample was pretreated with H_2O_2 (15%) and $Na_4P_2O_7$ (0.1 mol L^{-1}), and then its particle-size distribution was determined using the pipette method (Lu, 1999).

At each gas measurement, soil samples (0–20 cm) were collected from three randomly-selected points near each collar, excluding the collars in the trenched subplots, and thoroughly mixed for determining soil moisture content, water soluble organic C (WSOC) and microbial biomass C (MBC) concentrations. The soil moisture content was determined by the difference in mass after drying at 105 °C until constant weight. Soil WSOC was measured following Wu et al. (2010). Briefly, a portion of fresh sample equivalent to 20 g oven-dry soil was placed into a 100 mL centrifuge tube, and then 40 mL of distilled water was added. The mixture was shaken for 30 min at a speed of 120 rpm at 25 °C. Then, the mixture was filtered through a 0.45 μm membrane filter (Millipore Corp., USA). The WSOC in the filtrate was analyzed on an automated TOC-TN analyzer (Shimadzu, TOC-Vcph, Japan).

The chloroform fumigation-extraction method was used to measure the soil MBC concentration (Vance et al., 1987). The K_2SO_4 solution (0.5 mol L^{-1}) was used to exact C from the fumigated and control (non-fumigated) soil samples in a 1:2.5 (w:v) mixture of soil and extractant. Then, the extract was filtered through a 0.45 μm membrane filter (Millipore Corp., USA), and the C concentration in each filtrate was measured on an automated TOC-TN analyzer (Shimadzu, TOC-Vcph, Japan). The soil MBC concentration was calculated by the difference in the amount of C extracted between the fumigated and unfumigated soil (Wu et al., 1990).

2.5. Data and statistical analysis

R_S components were calculated as follows.
R_S = Measured values of soil collars in control plot
R_H = Measured values of soil collars in trenched plots

$$R_A = R_S - R_H$$

Annual cumulative soil CO_2 emission was calculated as

$$M = \Sigma\ (R_{i+1} + R_i)\ /2 \times t_{i+1} - t_i) \times 3600 \times 24 \times 44 \times 10^{-8} \tag{1}$$

where M is the cumulative value of soil CO_2 emission (t CO_2 $ha^{-1}\,yr^{-1}$), R is the soil respiration rate (μmol $m^{-2}\,s^{-1}$), i is the sampling number, and t is the sampling time based (Julian day).

An exponential model was adopted to present the relationship between R_S components and soil temperature:

$$y = a \times e^{k \times t}, \tag{2}$$

where y is the soil CO_2 efflux rate of soil respiration components (μmol $m^{-2}\,s^{-1}$), t is soil temperature, and a and k are constants.

The temperature sensitivity of soil CO_2 efflux (Q_{10}) was calculated by

Table 1
Selected chemical and physical properties (means with SD in parentheses) of soils (0–20 cm layer) in the evergreen broadleaf forest and Moso bamboo plantation (n = 3).

Land-use type	pH	Bulk density (g cm^{-3})	Organic C	Total N	Sand	Silt	Clay	Available P	Available K
					(g kg^{-1})			(mg kg^{-1})	
Evergreen broadleaf forest	5.78 (0.13) a[†]	1.02 (0.09) b	18.8 (1.4) a	1.91 (0.07) b	347 (24) a	381 (26) a	272 (16) a	8.14 (0.37) b	87.6 (4.9) a
Moso bamboo plantation	5.59 (0.11) a	1.18 (0.10) a	16.9 (1.1) b	2.31 (0.09) a	368 (24) a	372 (18) a	260 (38) a	9.27 (0.47) a	93.5 (4.1) a

[†] Means with different letters indicate significant differences between different land-use types for each parameter at P = 0.05, based on the least significant difference (LSD) test.

$$Q10 = e^{10 \times k} \tag{3}$$

A repeated-measures analysis of variance (ANOVA) was used to assess significance of the impact of land-use type, season of sampling, and their interaction on R_S components, soil temperature, moisture content, and WSOC and MBC concentrations. A one-way ANOVA and the least significant difference (LSD) test were performed to determine statistical significance of land-use conversion effects on mean annual CO_2 flux, annual cumulative CO_2 flux, and Q_{10}. Before conducting the ANOVA, the normality and homogeneity of variance were tested and appropriate transformations were conducted in case some of the data did not meet those assumptions. The significance was determined at an alpha level of 0.05 for all statistical analyses, unless otherwise mentioned. The statistical analyses were performed using SPSS version 18.0 (SPSS, Chicago, IL, USA).

In addition, the relationship between R_S components and soil moisture content, and WSOC and MBC concentrations were analyzed using linear regression.

3. Results

3.1. Land-use change effects on soil physicochemical properties and environmental parameters

The evergreen broadleaf forest and bamboo plantation differed significantly in soil total N, available P and bulk density, and soil organic C (Table 1), implying that land-use change had significant effects. No effect of land-use change on soil pH, available K, and texture was observed (Table 1). A distinct seasonal variation in soil temperature was observed regardless of land-use type (Table 2 and Fig. 2a), and land-use change did not affect soil temperature (Table 2). In addition, the interactive effect of land-use type and sampling season on the soil temperature was significant (Table 2). A distinct seasonal variation in soil moisture content was observed regardless of the land-use type (Table 2 and Fig. 2b). There was no effect of land-use or land-use by sampling season interaction on soil moisture content. The soil moisture content in the broadleaf forest and bamboo plantation averaged 316 and 304 $g\ kg^{-1}$, respectively, and its lowest value was found in July for both land-use types.

During the full two years, land-use, season and land-use by sampling season interaction significantly affected soil WSOC and MBC (Table 2). The WSOC concentration in the bamboo plantation was higher than that in the broadleaf forest (Fig. 2c). The WSOC concentration was relatively low between February and March in each year, especially in the broadleaf forest. The WSOC concentration in both the broadleaf forest and the bamboo plantation was at the highest in June. MBC concentration in the broadleaf forest was higher than that in the bamboo plantation during most of the experimental period (Fig. 2d).

3.2. Land-use change effects on seasonal variations of soil respiration components

Over the two years, land-use type, season, and their interaction significantly affected all R_S components (Table 2). The temporal variation of the rate of those components was smaller in the broadleaf forest than in the Moso bamboo plantation, with the rates mostly lower in the former than in the latter (Fig. 3a–c). The R_S and R_A were similar in temporal pattern from July through September, with some peaks, whereas January through March had some small values. The highest R_S and R_A for the two land-use types were observed in July. The highest R_H was found in September, which was different from the seasonal pattern of R_A and R_S. The mean annual and annual cumulative R_S and R_H in the bamboo plantation were greater than those in the broadleaf forest (Table 3), while no significant difference in those of R_A were observed between the two land-use types. In the two-year experimental period, following the conversion of the evergreen broadleaf forest to the Moso bamboo plantation, the mean annual R_S, R_A and R_H were increased by 19.5%, 12.0% and 23.1%, respectively, and the annual cumulative R_S, R_A and R_H were increased by 18.8%, 15.1% and 20.9%, respectively.

3.3. Relationships between soil respiration components and soil environmental properties

Both soil R_A and R_H were exponentially related to soil temperature ($P < 0.01$), for both land-use types (Table 4). Soil temperature alone explained 48% and 79% of the variation in R_A and R_H, respectively, in the broadleaf forest, and 68% and 79%, respectively, in the Moso bamboo plantation. The Q_{10} for R_A was less than that for R_H in the broadleaf forest, and it was the opposite in the Moso bamboo plantation. Converting the broadleaf forest to bamboo plantation increased the Q_{10} for R_A ($P < 0.05$), but did not affect the Q_{10} for R_H.

Neither soil R_A nor R_H was correlated with soil moisture content, but both were correlated with soil WSOC concentration ($P < 0.01$), regardless of land-use type (Table 5). Soil R_H was positively related to soil MBC concentration in the broadleaf forest ($P < 0.01$), but not in the bamboo plantation (Table 5). Soil R_A was not correlated with soil MBC concentration, regardless of the land-use type (Table 5).

4. Discussion

To elucidate the effects of land-use change on soil properties and ecological functions, space-for-time substitution is regarded as an effective method and has been extensively used (Smith et al., 2002; Chen

Table 2
Significance of effects of land-use type, sampling season, and their interaction on soil temperature, soil moisture content, soil water soluble organic C (WSOC) concentration, soil microbial biomass C (MBC) concentration, and soil respiration components.

	Soil temperature	Soil moisture	WSOC	MBC	R_S	R_A	R_H
2013–2014							
Land-use type (df = 1)	ns[a]	ns	**	*	**	**	*
Season (df = 22)	**	**	**	**	**	**	**
Land-use type × season (df = 22)	**	ns	ns	*	**	**	**
2014–2015							
Land-use type (df = 1)	ns	ns	**	ns	**	*	**
Season (df = 22)	**	**	**	**	**	**	**
Land-use type × season (df = 22)	**	ns	**	**	**	**	**
Two years (2013–2015)							
Land-use type (df = 1)	ns	ns	**	*	**	*	**
Season (df = 45)	**	**	**	**	**	**	**
Land-use type × season (df = 45)	**	ns	**	**	**	**	**

[a] ns, not significant.
* Significant at $P = 0.05$ level.
** Significant at $P = 0.01$ level.

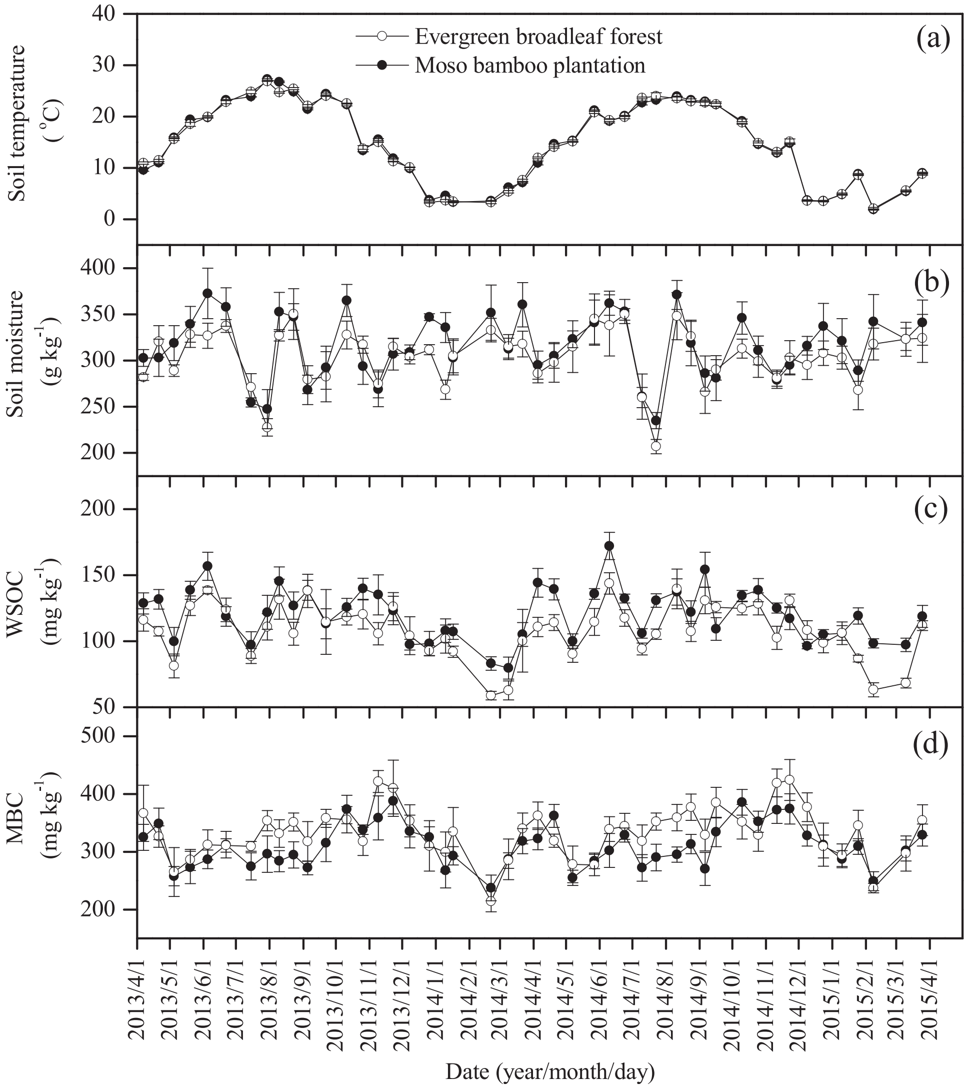

Fig. 2. Seasonal changes of (a) soil temperature at 10 cm depth, (b) soil moisture in 0–20 cm soil layer, (c) soil water soluble organic C (WSOC) concentration in that layer, and (d) soil microbial biomass C (MBC) concentration in that layer in the evergreen broadleaf forest and Moso bamboo plantation, from April 2013 to March 2015. Vertical bars are standard deviations of the mean (n = 3).

et al., 2004; Liao et al., 2012). The successful application of the space-for-time substitution approach is largely based on the assumption that the adjacent soils under different land-use types were originally similar in soil properties (Smith et al., 2002; Chen et al., 2004). In this study, the bamboo plantations were converted from natural broadleaf forests in 2002, and before the land-use change, all of the sites in this study were under natural broadleaf forests. The lack of significant differences between the broadleaf forest and the bamboo plantation in the sand, silt, and clay contents in the soil (Table 1) supports that assumption. Therefore, differences in soil properties and ecological functions between the broadleaf forest and the bamboo plantation were mainly attributed to changes in the land-use and related management practices.

4.1. Do soil R_A and R_H respond differently to land-use conversion?

Our results revealed that conversion from the broadleaf forest to the bamboo plantation in the subtropics increased mean annual and annual cumulative values of R_S and R_H, but did not change those of the R_A (Table 3). This finding rejects our first hypothesis that the converting the natural forest to a bamboo plantation increases both R_A and R_H and is consistent with the results of Shi et al. (2015), who reported that conversion of a mixed broadleaf Korean pine forest to Dahurian larch (*Larix gmelinii*) or Korean pine (*Pinus koraiensis*) plantations increased both R_S and R_H, but did not change R_A. Wang et al. (2013) also reported that R_S was increased by 25.2% and 21.7% following the conversion of natural broadleaf forests to *Pinus massoniana* Lamb. and *Michelia macclures* Dandy plantations, respectively. This finding is a step further from our previous study that reported an increase in soil CO_2 efflux after the land-use change from natural broadleaf forests to intensively managed Moso bamboo plantations (Liu et al., 2011), and suggests that such land-use change negatively affected the ability of C sequestration in forest ecosystems in terms of soil CO_2 efflux.

The increase in R_S after land-use change in our study was caused by the increase in R_H, since the R_A was not altered (Table 3), with the following three possible mechanisms. First, inorganic fertilizer applied in the bamboo plantation may have accelerated the mineralization of soil organic matter (SOM) (Mancinelli et al., 2010; Tu et al., 2013), and thereby increased R_H (Tu et al., 2013). Second, the practice of deep tillage in the Moso bamboo plantation could have reduced the stability of soil structure and enhanced the aeration in the soil profile (Abdollahi et al., 2014), subsequently increasing the exposure of SOC to soil microbial attack (Sainju et al., 2008). The present finding of a lower SOC concentration (Table 1) and higher concentration of WSOC (Fig. 2c) in the Moso bamboo plantation relative to those in the evergreen broadleaf forest gives strong evidence of the operation of the above two mechanisms. Since the WSOC is one form of the labile organic C pool with higher availability (Hassan et al., 2016), higher WSOC concentration in the Moso bamboo plantation than in the evergreen broadleaf forest would attribute to the fact of higher R_H in the Moso

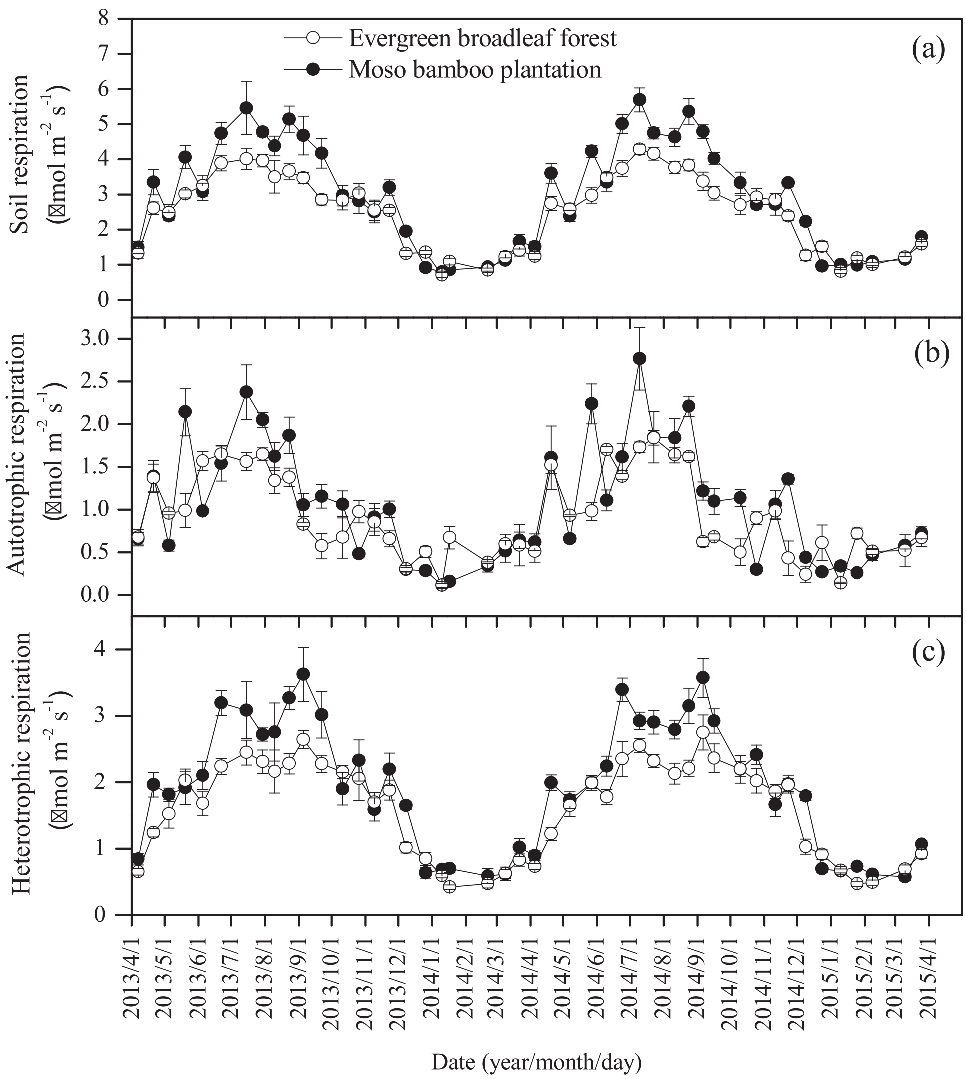

Fig. 3. Seasonal variations in (a) soil respiration, (b) autotrophic respiration, and (c) heterotrophic respiration rates in the evergreen broadleaf forest and Moso bamboo plantation.

Table 3
Comparison of mean annual values and annual cumulative values (means with SD in parentheses) of soil respiration (R_S), autotrophic respiration (R_A), and heterotrophic respiration (R_H) between evergreen broadleaf forests and Moso bamboo plantations (n = 3).

Land-use type	Mean annual CO_2 flux (μmol m^{-2} s^{-1})			Annual cumulative CO_2 flux (t CO_2 ha^{-1} yr^{-1})		
	R_S	R_A	R_H	R_S	R_A	R_H
			2013–2014			
Evergreen broadleaf forest	2.48 (0.09) b[†]	0.91 (0.04) a	1.57 (0.06) b	31.60 (1.42) b	11.51 (0.54) a	20.09 (0.97) b
Moso bamboo plantation	2.93 (0.09) a	1.01 (0.11) a	1.92 (0.07) a	37.25 (1.96) a	12.64 (0.77) a	24.61 (1.22) a
			2014–2015			
Evergreen broadleaf forest	2.55 (0.11) b	0.93 (0.16) a	1.62 (0.09) b	34.06 (1.56) b	12.40 (0.83) a	21.66 (0.96) b
Moso bamboo plantation	3.07 (0.13) a	1.05 (0.20) a	2.02 (0.07) a	40.75 (2.22) a	14.88 (1.44) a	25.87 (1.34) a
			Two years (2013–2015)			
Evergreen broadleaf forest	2.51 (0.10) b	0.92 (0.10) a	1.60 (0.06) b	32.83 (1.43) b	11.96 (0.65) a	20.88 (0.95) b
Moso bamboo plantation	3.00 (0.03) a	1.03 (0.08) a	1.97 (0.06) a	39.00 (2.04) a	13.76 (1.09) a	25.24 (1.03) a

[†] Means with different letters indicate significant differences between land-use types within each sampling period for each parameter at P = 0.05, based on the least significant difference (LSD) test.

bamboo plantation than in the evergreen broadleaf forest. Third, the practice of understory removal in the Moso bamboo plantation would slightly raise soil temperature (Zhao et al. 2012), thereby promoting the decomposition of SOM (Zhang et al., 2014).

The R_A can be altered by land-use change because land-use conversion usually changes factors such as rate of photosynthesis and the allocation of photosynthates from aboveground to belowground, root production and turnover, and plant phenology, which is closely associated with R_A (Kuzyakov and Gavrichkova, 2010; Tu et al., 2013; Balogh et al., 2015; Shi et al., 2015). The intensive management (fertilization and tillage) in the bamboo plantation would also influence R_A (Tu et al., 2013). The lack of land-use change effect on R_A in this study can be explained by the canceling out of the positive and negative effects of the aforementioned factors. Detailed mechanisms regarding land-use change effects on R_A need to be investigated in future studies.

Table 4
Relationships between soil respiration component and soil temperature (at 10 cm depth) in the evergreen broadleaf forest and Moso bamboo plantation.

Soil respiration	Evergreen broadleaf forest		Moso bamboo plantation	
	Model	Q_{10}	Model	Q_{10}
R_S	$Y = 0.90e^{0.061X}$ ($R^2 = 0.83$, $P < 0.01$)	1.84 b[†]	$Y = 0.89e^{0.073X}$ ($R^2 = 0.84$, $P < 0.01$)	2.08 b[*]
R_A	$Y = 0.33e^{0.057X}$ ($R^2 = 0.48$, $P < 0.01$)	1.78 c	$Y = 0.24e^{0.083X}$ ($R^2 = 0.68$, $P < 0.01$)	2.30 a[*]
R_H	$Y = 0.52e^{0.066X}$ ($R^2 = 0.79$, $P < 0.01$)	1.93 a	$Y = 0.59e^{0.070X}$ ($R^2 = 0.79$, $P < 0.01$)	2.00 c

† Different lowercase letters within a column indicate significant differences between different soil respiration components within the same land-use type at the $P = 0.05$ level based on the least significant difference (LSD) test.

* Indicates significant differences between the two land-use types within the same soil respiration component at the $P = 0.05$ level based on the least significant difference (LSD) test.

4.2. Do soil R_A and R_H respond differently to variations in environmental factors?

Soil temperature is one of the most important factors controlling the seasonal variation of both soil R_A and R_H (Zhang et al., 2013; Yan et al., 2015a; Chang et al., 2016; Wang et al., 2017). In this study, soil temperature alone explained a greater percent of variation in R_H than in R_A in both the broadleaf forest and the bamboo plantation (Table 4), likely because R_A greatly depends on the status of root carbohydrates, which is strongly affected by plant traits such as leaf photosynthesis and transport of carbohydrates from aboveground to belowground plant tissues (Li et al., 2013a), weakening the dependence of R_A on soil temperature.

The Q_{10} values for R_S and its components have been found to vary greatly between land-use types (Wang et al., 2010; Adewopo et al., 2015; Chang et al., 2016); however, it is still unclear if the Q_{10} values of R_A and R_H respond differently to land-use conversion. In our study, Q_{10} for R_S, R_A and R_H in the broadleaf forest (1.78–1.93) and bamboo plantation (2.00–2.30) were similar to results from other subtropical forests (Yi et al., 2007; Wang et al., 2017). The opposite pattern of Q_{10} for R_A vs. R_H in both the broadleaf forest and the bamboo plantation (Table 4) suggests that R_A and R_H respond differently to the increase of soil temperature, confirming our second hypothesis that soil R_A and R_H respond differently to variation in environmental factors, i.e. soil temperature. No consensus has been reached on the question of whether R_A or R_H has greater temperature sensitivity (Hartley et al., 2007; Yan et al., 2015a; Wang et al., 2017). For example, Boone et al. (1998) found greater Q_{10} (4.6) for R_A than for R_H (2.5) in a mixed temperate forest. Luan et al. (2011) reported that Q_{10} for R_H was greater than that for R_A in an oak (*Quercus nigra*) chronosequence, regardless of stand age, but Yan et al. (2015a) observed no significant difference in Q_{10} between R_A and R_H in a poplar (*Populus tomentosa*) plantation chronosequence, regardless of stand age. Therefore, we conclude that the answer to the question of whether R_A or R_H has greater temperature sensitivity will vary greatly with land-use type or climate conditions. The difference of Q_{10} with land-use type and different Q_{10} values for R_A and R_H will cause uncertainty in cumulative R_S estimation (Luan et al., 2011). Thus, partitioning of R_S into R_A and R_H components is important to synthesize Q_{10} observations, which is helpful to estimate change of R_S under global climate warming.

We found that neither R_A nor R_H was correlated with soil moisture content, regardless of land-use type, rejecting part of the second hypothesis; this result was likely because soil moisture contents in the broadleaf forest and bamboo plantation were relatively high, and the temporal variation was small because of abundant precipitation in the study region. Consequently, soil moisture was not a limiting factor for soil microbial activity and R_H (Mo et al., 2008; Sheng et al., 2010; Zhang et al., 2014).

The labile organic C can be easily decomposed by microorganisms (Lundquist et al., 1999; Iqbal et al., 2010), and thus the soil labile organic C pool is closely associated with the rate of soil CO_2 efflux (Iqbal et al., 2010; Luo et al., 2011; Hassan et al., 2016; Chen et al., 2017). The WSOC is one form of the labile organic C pool with higher availability (Hassan et al., 2016), and has been observed to have a positive relationship with R_S (Wang et al., 2014; Zhang et al., 2015; Hassan et al., 2016). Possible reasons for the positive relationship between both R_A and R_H and WSOC, regardless of land-use type (Table 5), are: 1) WSOC content is closely related to SOM mineralization, which is the main pathway for forming heterotrophic respiration (Uchida et al., 2012); and 2) part of the WSOC originates from carbohydrates secreted from plant roots, which is closely linked to autotrophic respiration (Li et al., 2013a). In addition, the positive relationship between R_H and MBC but lack of relationship between R_A and MBC (Table 5) further supports the above analysis and is in agreement with Wang et al. (2017). Therefore, the partition of R_S into R_A and R_H is essential for elucidating the microbial mechanism involved in soil respiration.

4.3. Does land-use conversion alter relationships between soil respiration components and environmental factors?

Relationships between R_S and environmental factors vary by land-use type (Nazaries et al., 2015; Chang et al., 2016; Guo et al., 2016). For example, Sheng et al. (2010) found significant relationships ($P < 0.01$) between R_S and soil moisture content in a natural forest, citrus orchards, and sloping tillage land, but not in Chinese fir (*Cunninghamia lanceolata*) and *Schima superba* plantations. Our results on the Q_{10} values for both R_S and R_A and the differed relationship between soil R_H and MBC in the two land-use systems (Table 5) indicate that the relationship between R_S components and environmental factors depends on the land-use type and associated management practices, therefore supporting our third hypothesis.

Table 5
Relationships between soil respiration components and soil moisture, soil water soluble organic C (WSOC) concentration, and soil microbial biomass C (MBC) concentration in the evergreen broadleaf forest and Moso bamboo plantation. The R^2 and P values are presented only when $P < 0.05$.

Land-use type	Soil moisture (mg g^{-1})	WSOC (mg kg^{-1})	MBC (mg kg^{-1})
R_S (μmol m^{-2} s^{-1})			
Evergreen broadleaf forest	$Y = -0.0024X + 3.24$	$Y = 0.028X - 0.53$ ($R^2 = 0.29$, $P < 0.01$)	$Y = 0.056X + 0.65$
Moso bamboo plantation	$Y = -0.01X + 6.16$	$Y = 0.034X - 1.05$ ($R^2 = 0.19$, $P < 0.01$)	$Y = -0.0002X + 3.06$
R_A (μmol m^{-2} s^{-1})			
Evergreen broadleaf forest	$Y = -0.0001X + 0.96$	$Y = 0.007X + 0.16$ ($R^2 = 0.10$, $P < 0.01$)	$Y = 0.007X + 0.70$
Moso bamboo plantation	$Y = -0.0037X + 2.24$	$Y = 0.011X - 0.31$ ($R^2 = 0.11$, $P < 0.01$)	$Y = -0.0011X + 1.42$
R_H (μmol m^{-2} s^{-1})			
Evergreen broadleaf forest	$Y = -0.0022X + 2.28$	$Y = 0.021X - 0.69$ ($R^2 = 0.36$, $P < 0.01$)	$Y = 0.005X - 0.053$ ($R^2 = 0.10$, $P < 0.01$)
Moso bamboo plantation	$Y = -0.0062X + 3.91$	$Y = 0.022X - 0.74$ ($R^2 = 0.21$, $P < 0.01$)	$Y = 0.0009X + 1.64$

Possible mechanisms for the change in relationships between R_S and environmental factors caused by land-use change are that vegetation coverage and associated management practices altered by such conversion may strongly modify soil physicochemical or biochemical properties, thereby affecting soil CO_2 production (Nazaries et al., 2015; Zhang et al., 2015; Chang et al., 2016). Larger Q_{10} values of R_S and R_A in the bamboo plantation than in the broadleaf forest (Table 4) demonstrate that the land-use change enhanced the temperature sensitivity of R_S. The possible mechanisms would be (1) various management practices, mainly deep tillage, application of chemical fertilizer and removal of forest floor vegetation, greatly enhanced plant root growth and increased soil microbial activity, and consequently increased soil CO_2 emission through soil organic C mineralization and root respiration (Adewopo et al., 2015; Zhang et al., 2015); (2) the fine root biomass of bamboo forests has been found to be much larger than that of broadleaf forests, and both growth and turnover rates of bamboo fine roots were faster than that of broadleaf forests (Liu et al. 2013). Those factors would affect the temperature sensitivity of R_S; (3) the management practices applied in the bamboo forest decreased the stability of SOM (Li et al., 2013b), which may increase the seasonal fluctuation of R_S.

5. Conclusions

Converting natural evergreen broadleaf forests to Moso bamboo plantations substantially increased annual R_S and R_H, and Q_{10} of R_S and R_A. We conclude that the studied land-use change decreased the potential for soil C sequestration due to increased soil CO_2 emission. If such land-use change effect on soil CO_2 emission is confirmed in the wider subtropical area in future research, then we will be certain that conversion from natural forests to intensively managed plantations reduces soil C sequestration or the potential to mitigate climate change by forest ecosystems. More importantly, our results clearly demonstrated that soil R_A and R_H responded differently to land-use change and variations in environmental factors, and land-use conversion modified relationships between R_S components and environmental factors. This suggests that partitioning of R_S into its components is essential to elucidate mechanisms associated with changes in R_S caused by land-use change and to predict R_S under various climate scenarios.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.01.003.

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